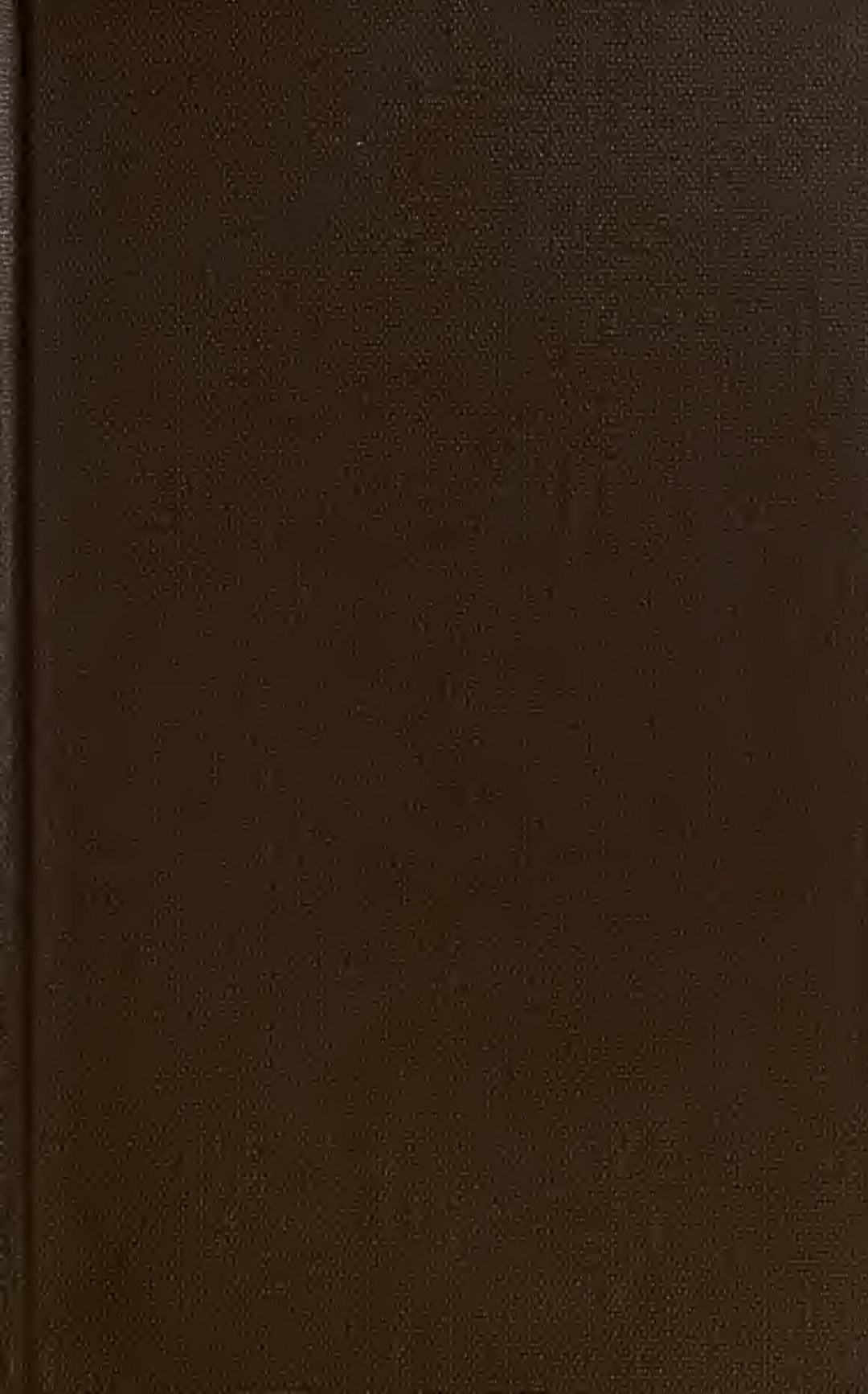




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Morphology and Arrangement of Meromes in *Ischadites dixonensis*, an Ordovician Receptaculitid

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ABSTRACT

Ischadites dixonensis (Miller and Gurley, 1896), from the Ordovician Galena Group of Illinois, is the oldest described North American ischaditid. The holotype is exceptionally well preserved and provides information on merome head morphology, articulation, and arrangement on the surface of the thallus. Meromes occur in whorls and form an equal number of dextral and sinistral parastichies. Each parastichy begins either at one of the heads surrounding the basal pole or at a triangulum, and extends to the margin of a clearly demarcated apical lacuna. The unusually complete morphological characterization that is now available for *I. dixonensis* will play an important role in discussions of receptaculitid morphogenesis and orientation.

INTRODUCTION

It has become increasingly clear, through the work of Rietschel (1969), Campbell et al. (1974), and Gould and Katz (1975), that an accurate description of the shape and arrangement of the elements making up the surface of the thallus of receptaculitids is a prerequisite for any definitive analysis of their morphogenesis and taxonom-

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ic affinities. These aspects of morphology have been particularly difficult to observe due to preservational problems and incomplete calcification of original structures. *Ischadites dixonensis* offers an unusual opportunity to provide this information because calcified meromes were present over nearly the entire surface of the thallus, and because the holotype (and only available specimen) is unusually well preserved (fig. 1). Since its original description and illustration do not adequately represent its detailed morphology, we believe the present redescription is necessary. Our treatment of *I. dixonensis* differs from that of Miller and Gurley in: 1) concentrating on the morphology and arrangement of merome heads; 2) providing new information on internal structure; 3) reversing the life orientation of the thallus; and 4) interpreting receptaculitids as algae rather than sponges.

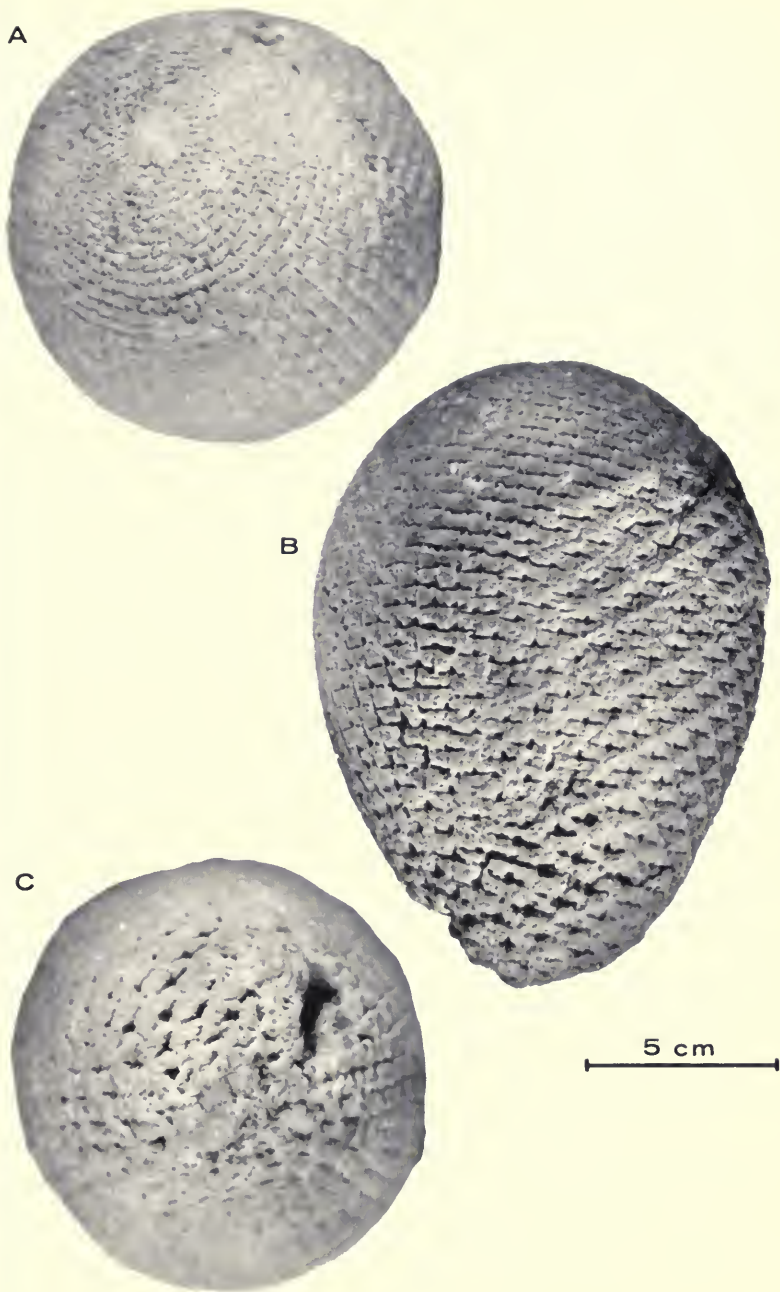
I. dixonensis is the oldest North American species thus far described that can be unequivocally assigned to the genus *Ischadites*. Initial study of "*Ischadites*" *iowensis*, a common receptaculitid from the Galena Group in the tri-state area of Illinois, Iowa, and Wisconsin, indicates that it should not be considered a member of this genus. *I. dixonensis*, on the other hand, is a "good" ischaditid, and in many respects is similar to the genotype, *I. koenigii*, from the Silurian of North America and Europe.

MATERIAL

The specimen described here was collected in Middle Ordovician, dolomitized, crinoidal biosparites of the basal Galena Group, near Dixon, Illinois, U.S.A. It is preserved as a dolomitized mold of the calcified portions of the thallus. It consists of an incomplete (either partially lost or never entirely collected), "external," concave portion bearing an impression of the abaxial surfaces of merome plates, and an "internal," convex portion formed of material deposited between the meromes (preserving an impression of the merome shafts and of the adaxial surfaces of merome heads) and within the central axis.

Opposite:

FIG. 1. *Ischadites dixonensis* (Miller and Gurley, 1896), FMNH UC 6053, Gurley Collection, University of Chicago Collection, housed in Field Museum of Natural History. A, apical view; B, lateral view; height of thallus: 4.3 cm.; maximum diameter of thallus: 3.1 cm.; C, basal view.



MORPHOLOGY

Our use of terminology assumes that receptaculitids were algae. We will not, at present, argue this assignment; rather, we will rely upon present consensus on this point (Byrnes, 1968; Nitecki, 1969, 1970, 1972; Rietschel, 1969; and Campbell et al., 1974). Likewise, we will defer discussion of the orientation and morphogenetic interpretation of the thallus. It suffices for now to state that our orientation coincides with that made by Nitecki (1969, in part), Rietschel (1969), and in the main body of the text of Gould and Katz (1975). It is opposite, however, to that made in the "note added in proof" of Gould and Katz and by Byrnes (1968) and Nitecki (1969, in part; 1971; 1972).

Thallus shape: The thallus of *I. dixonensis* is ovoid, with its greatest transverse diameter located closer to the summit than to the base (figs. 1B, 2 insert). Its surface is more regular than that of other members of this genus, and could almost be described as that of a solid of revolution (generated by the revolution of an oval about its major axis). It nevertheless shows subtle indication, especially near the summit of the thallus, of the helical surface topography which is so typical of *I. koenigii*. The sense of this helix is dextral if it is followed in lateral view upward from the oldest to the youngest portions of the plant. Since the shape of the central axis is poorly known, it is not clear whether this is simply a surficial reflection of a topographically similar central axis, or whether it is superimposed on a regular axis through systematic variation in the length or orientation of meromes. Associated with this twist is a displacement of the apical and basal poles relative to each other and to the longitudinal topographic axis of the thallus. If the apical and basal poles are defined as passing through the center of merome plate whorls that are very near their respective ends of the thallus, and as perpendicular to planes described by those whorls, then each pole is inclined at about 20° to the longitudinal topographic axis.

The basal portion of the thallus (fig. 1C) is not as well preserved as the rest of the surface, but it seems that it was almost completely covered by merome plates. The preserved impressions of plates indicate that if a pedicle-like structure existed here, it must have had a diameter less than 2 mm. In all probability, a pedicle with holdfast was present at least in very young individuals. During growth of the thallus, this pedicle either remained small and was closely sur-

rounded by the developing heads of the first (oldest) meromes, or else was eventually completely occluded by the growth of these heads. The former alternative certainly involves the more conventional conception of algal anatomy, and has an analog in the extant dasyclad *Bornetella sphaerica*. However, the latter alternative is descriptive of the condition of well-preserved *I. barrandei* (generally similar to *I. dixonensis*), in which neither a pedicle nor any opening for it is observed. In any case, there is no evidence for the presence of an opening such as Miller and Gurley (1896) described and identified as an osculum. The only hole in this part of the thallus has an irregular outline (fig. 1C), is not centered on the basal pole, and is evidently the result of fracturing either during the weathering out of the specimen or during collection.

The other end of the thallus is more completely preserved and presents fewer problems of interpretation. Articulated, calcified meromes extend to within 2.1 mm. of the apical pole. Adapically of this well-defined circle, composed of a single whorl of meromes, there are no impressions preserved. In this region the matrix forming the "internal" mold is continuous with that of the "external" mold, producing a narrow isthmus (diameter: 4.2 mm.) that was broken when the molds were separated. We interpret these observations as indicative of an apical lacuna in the original calcified cortex of the thallus. The existence of such an "opening" has been both postulated (e.g., Gould and Katz, 1975) and denied (e.g., Rietschel, 1969), but preservation of other taxa has not been adequate to settle the point.

In our present interpretation, the margin of the apical lacuna is formed by the most recently calcified meromes that were sufficiently well articulated with their neighbors to remain in place after the death of the alga and during the infilling of its "skeleton." Adapically from this margin, on the living plant, we would expect meromes that were either incompletely articulated, incompletely calcified, or both. These meromes probably surrounded an apical tuft of photosynthetic filaments protruding beyond the general surface of the thallus. A distinctive feature of *I. dixonensis* is that the zone on the thallus surface represented by well-calcified and articulated meromes comprises such a large portion of its total surface, or, in other words, that the apical lacuna is relatively small. As a contrast, *I. barrandei* is frequently preserved as a rather shallow "hemisphere," representing only the basal portion of the thallus. This con-

dition of preservation probably indicates a more limited surficial extent of well-calcified and articulated meromes. In this respect, *I. koenigii* is intermediate between these two species, although it is closer to *I. dixonensis*.

Central axis: An irregular fracture obliquely truncates the basal portion of the "internal" mold of the thallus. Removal of this basal fragment reveals a cross-section of the thallus from about the seventh to the seventeenth merome whorl. A maximum value for the width of the central axis at this level can be estimated from the inward extent of the molds of merome shafts outcropping on the surface of the fracture. The axis is certainly not wider than 6 mm. (one-fourth the total width of the thallus at this level) and is probably not wider than 5 mm. The uncertainty of this estimate is due primarily to the fact that the central portion of the "internal" mold is more open-textured than the periphery. Therefore, the molds of merome shafts simply become indistinguishable proximally, without clearly exposing their contact with the central axis. The merome shafts exposed by the fracture described above are straight and extend perpendicularly to the surface of the thallus. They are cylindrical and relatively thin throughout their observable length, showing no evidence of either distal or proximal expansions. At the distal end of the merome shaft, just where it joins its plate, its adapical surface is marked by a small pit (which may be drawn out as a trough on the adaxial surface of the plate) for the reception of the tip of the abapical rib (fig. 3) of the stellate structure of another merome (see below). It is important to note that this relationship is distinct from what Rietschel (1969) describes as a pit and rib insertion involving the abapical surface of the merome shaft and an adapical rib.

Merome heads: The merome heads of *I. dixonensis* are extremely similar to those of the Silurian *I. tenuis* (Nitecki and Dapples, 1975). They consist of a thin, marginally tapering plate whose abaxial surface is somewhat convex, closely associated with a four-ribbed stellate structure (fig. 3). The two latitudinal ribs have their bases at the distal end of the merome shaft and are in contact with the adaxial surface of the plate until shortly before reaching the plate margin. They are oriented 80-85° from the merome shaft and extend beyond the margins of the plate by approximately one-third of their length. The abapical meridional rib is similar to the latitudinal ribs in all respects, except that it is more nearly perpendicular to the merome

shaft and extends beyond the margin of its plate for nearly one-half its length. The adapical meridional rib is also nearly perpendicular to the merome shaft, and its base is located proximally on the shaft about one rib diameter from its mates. Its length relative to the plate margin (determined where the "internal" mold appears incomplete or abraded) is similar to that of the latitudinal ribs.

The most common type of merome plate is rhombic in outline (fig. 2), with the vertices pointing latitudinally and longitudinally. The largest rhombic plates (width: 4.4 mm.) occur at about the level of the fourteenth whorl, well below the topographic equator. Size of plates decreases toward both poles, with the smallest plates located nearest the apical pole. Accompanying this size gradient is a gradient in the shape of the rhombic plates. Near the apical pole they are relatively narrow longitudinally, while nearer the equator they become broader and then maintain a relatively constant shape. The surface of the "external" mold is too coarse to discern whether any growth lines were present on the plates.

The two other types of merome plates, *interposita* and *triangula* (a term introduced here for the plate situated directly adapically of an *interpositum*), are of the usual ischaditid form (Rietschel, 1969; Gould and Katz, 1975). The *interposita* are broader longitudinally than the rhombic plates of their own whorl, while the *triangula* are usually narrower than their rhombic neighbors.

Articulation of merome heads: In order to discuss the articulation of adjacent merome heads, it is useful to extend the analogy between the thallus and a terrestrial globe, by use of the cardinal directions. If we consider an array of rhombic plates only, the plates of one whorl can be conceived of as a series of eastern or western neighbors. Near the apical pole these neighbors touch each other only at their eastern and western vertices. However, in the equatorial and basal regions of the thallus, the plates are positioned slightly en eschelon, so that a given plate contacts its western neighbor only on a very short stretch of its northwestern edge, and its eastern neighbor on a very short stretch of its southeastern edge. There is no evidence of imbrication of plates within a whorl. Each plate also has neighbors to the southwest, southeast (members of the whorl formed immediately before), northwest, and northeast (members of the whorl formed immediately after), with each of which it shares large stretches of its respective edges (fig. 2). These plates of consecutive whorls imbricate in such a way that the plates of later-formed

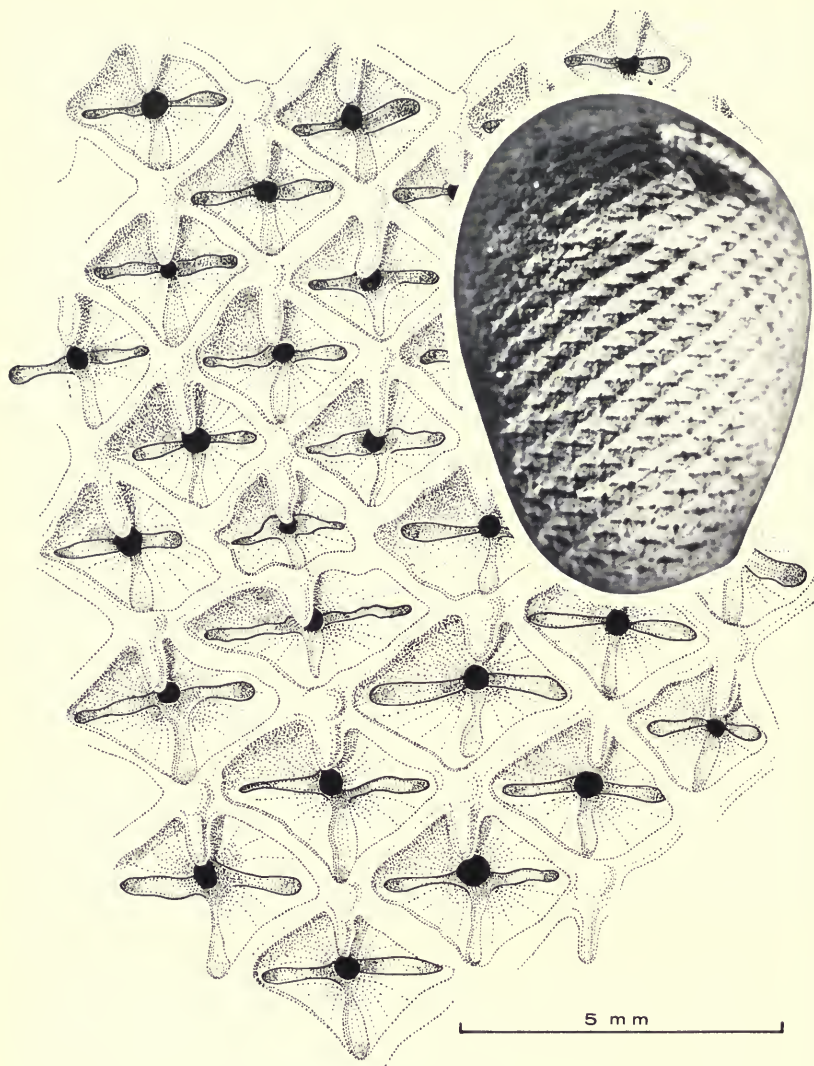


FIG. 2. Camera lucida drawing of a portion of the surface of *Ischadites dixonensis* (see fig. 4 for precise location). Insert: lateral view of *I. dixonensis*.

whorls underlie (or are situated adaxially to) the plates of earlier formed whorls. Finally, each rhombic plate has neighbors directly to the south and north, members of the second previous and second subsequent whorls. Where en eschelon and imbricate relationships are clearly developed, these plates do not come into direct contact at

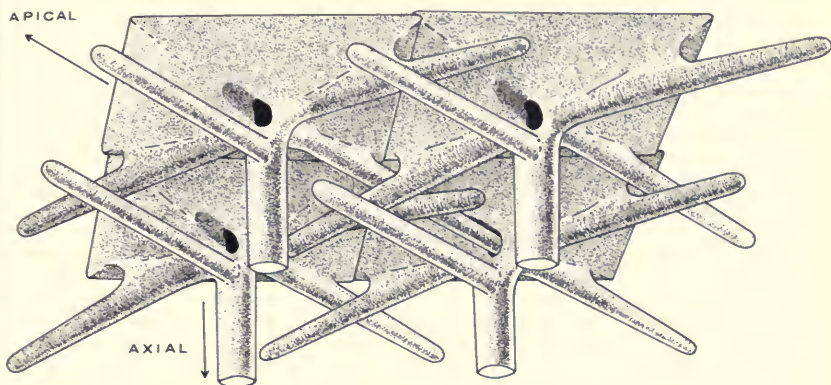


FIG. 3. Reconstruction of distal portion of meromes of *Ischadites dixonensis*, seen in oblique view (orientation shown by the arrows).

all; nearer the apical pole they may contact one another at a point. All of these relationships seem to involve only abutment and supraposition. There is no evidence of marginal sutures or fusion. In fact, as long as the plates were growing (by marginal accretion, if they were similar to the plates of *I. barrandei*; Rietschel, 1969; Gould and Katz, 1975), they could not have been fused.

The articulation of merome plates is maintained by a uniform pattern of interlocking of the ribs of stellate structures of neighboring heads (fig. 3). The abapical meridional rib extends all the way to the merome shaft of its southern neighbor, where its distal end inserts in the small pit located at the junction of the merome shaft and plate. The western latitudinal rib, with its distally adaxial orientation, passes adaxially of the abapical rib of its northwestern merome neighbor. Similarly, the eastern latitudinal rib passes adaxially of its northeastern neighbor's abapical rib. Furthermore, the eastern rib of one merome consistently lies adapically of the western rib of its eastern neighbor. These ribs overlap considerably, but at most extend only about three-fourths of the way to their neighbor's shaft. Finally, the adapical meridional rib extends adaxially of the abapical rib of its northern neighbor (also adaxially of the juxtaposed latitudinal ribs), to some point near the merome shaft of that neighbor. The relative position of the ribs of stellate structures is actually much more consistent throughout the thallus than the plate edge relationships originally used to define neighbors. It is in light of these interlocking relationships that the various details of merome head morphology find at least part of their explanation.

A similar pattern of merome head relationships is developed in the vicinity of interposita and triangula. The difference is that the northern neighbor of the interpositum, the triangulum, is a member of the first subsequent whorl rather than the second, and contacts it along an edge rather than not at all. Since the interpositum and triangulum each have only one stellate structure (not a universal feature of receptaculitids), similar to that of rhombic plates, the normal pattern of rib interlocking is preserved. However, the northwestern and northeastern neighbors of the triangulum (the first rhombic plates of the intercalated parastichies—see below) have no immediate southern neighbors. Therefore, their abapical ribs do not contact any merome shaft, but rather, terminate before crossing the latitudinal ribs of the associated interpositum.

Arrangement of meromes: Because of the limited exposure of merome shafts, the arrangement of meromes can only be studied in terms of the arrangement of their heads. For this specimen, it is possible to count and describe the position of heads over virtually the entire thallus. As shown by Gould and Katz (1975) for *I. barrandei*, the meromes of *I. dixonensis* are arranged in whorls (49, from basal pole to apical lacuna). At any latitude of the thallus a series of plates obtained by following consecutive western (or eastern) neighbors around the thallus always returns to the plate at which it began. This is an important distinction from other receptaculitids (e.g., certain specimens referred to *I. koenigii* in Nitecki, 1969) where, in the region of the apical hemisphere, other arrangements occur.

One of the most salient features of merome head arrangement is the pattern of sinistral and dextral spirals. These spirals apparently represent only conspicuous alignments of elements in a uniform pattern, rather than real morphogenetic units (Gould and Katz, 1975). In order to avoid confusion with the term for a series of sequentially produced elements ("genetic spiral" or "fundamental spiral"), we introduce the term "parastichy." This term is commonly used in literature on phyllotaxis and denotes a series of elements, within a uniform array, in which consecutive members can be recognized inductively by some regular spatial transposition (Williams, 1974). We will be dealing primarily with series of plates that are juxtaposed along a considerable length of their edges. Although these actually are only a subset of all possible parastichies, and technically should be called "contact parastichies," the less precise term can be used, in this case, without confusion. For example, the dextral para-



FIG. 4. Schematic map of relative plate positions on the basal hemisphere of *Ischadites dixonensis*. Plates whose outlines are clearly preserved on the specimen are shown as dots. Less clearly determinable outlines are indicated by small circles. Concentric circles define the basal 25 whorls of the thallus, within which all interposita and triangula are located. The irregular region enclosed by the solid line surrounding the basal pole is the area that is incompletely preserved. The similarly circumscribed region extending from the twelfth to the twenty-second whorl is shown in Figure 2. Broken lines indicate several arbitrarily chosen parastichies. Orthostichies are numbered around the circumference of the map, and, for ease of reference, actual plate positions have been shifted to align the orthostichies along radii. This makes the parastichies and the spacing between meromes appear less regular than on the actual specimen.

stichy to which a given plate belongs would be composed of 1) that plate, itself; 2) the plate, if it exists, that is a southwestern neighbor of 1, and all succeeding southwestern neighbors; and 3) the plate, if it exists, that is a northeastern neighbor of 1, and all succeeding

northeastern neighbors. Defined in this way, all parastichies on *I. dixonensis* begin (i.e., have their oldest element) either with one of the meromes immediately surrounding the basal pole or with one bearing a triangulum. All triangula on this specimen occur in the basal hemisphere of the thallus (precise positions are given in fig. 4). Since each merome can be seen as an element of both a dextral and a sinistral parastichy, each of these points of inception is the beginning of both a dextral and a sinistral parastichy. Furthermore, each parastichy anywhere on the thallus continues all the way to the margin of the apical lacuna. A consequence of this is that an equal number of dextral and sinistral parastichies pass through any given whorl of the thallus.

An alternate characterization of the surficial pattern of *I. dixonensis* is as a group of orthostichies, which in this case are series of northern or southern neighbors (meridional series). Each plate is a member of only one orthostichy, and, except for interposita and their associated triangula, any orthostichy includes only plates belonging to alternate whorls. Each orthostichy extends to the margin of the apical lacuna and begins either with one of the plates immediately surrounding the basal pole, with the northwestern neighbor of a triangulum, or with the northeastern neighbor of a triangulum. The number of orthostichies is equal to the sum of the dextral and sinistral parastichies. Whether the surficial pattern is perceived as a system of orthostichies or parastichies depends on the extent of calcification and manner of preservation. When plate boundaries are evident, parastichies are usually most conspicuous. When only the pattern of stellate structures is clearly exposed orthostichies are more pronounced. Thus, although these two expressions of pattern are redundant, each is useful in a different setting. Both were necessary for the complete interpretation of the present specimen (see fig. 1B).

Another significant aspect of merome arrangement is the number of plates surrounding the basal pole. We estimate this from the number of interposita on the thallus and the maximum number of meromes per whorl (or alternately, from the number of meromes in any whorl and the number of interposita situated abapically of that whorl). Since: 1) for each interpositum, an additional merome occurs in subsequent whorls; 2) there are clearly 31 meromes per whorl in the apical portion of the thallus; and 3) we have located 21 interposita on the thallus, there can be no more than 10 meromes immediately surrounding the basal pole. Given the extent of the inade-

quately preserved area, we may well have missed two interposita, but probably not more than four. Therefore, it is unlikely that there are fewer than six meromes around the basal pole, and there are certainly no more than 10.

DISCUSSION

In most respects, the description we have presented of *I. dixonensis* is consistent with that offered by Rietschel (1969) for forms similar to *Receptaculites neptuni*. Conspicuous differences involve our demonstration of: 1) an apical lacuna that seems to be too clearly demarcated to presume that it occurs only because of breakage or inadequate preservation; and 2) a uniform pattern of penetration of merome shafts by the abapical rib of their northern neighbor. Of the features of the two descriptions that are more similar, several seem to be characteristic of an even broader range of receptaculitid taxa. These include the order of juxtaposition and overlap between the latitudinal and meridional ribs of stellate structures, the direction of imbrication between consecutive merome whorls, the arrangement of interposita and triangula, and the geometry of origin of new parastichies. We must emphasize, however, that there are receptaculitids that depart significantly from certain aspects of this general pattern. These will be considered in detail elsewhere.

In addition to simply describing the morphology of *I. dixonensis*, we have tried to set up a procedure and terminology for expressing the arrangement of meromes on the thallus. This has been designed to allow more precise descriptions of the manner in which the number of meromes at any particular latitude on the thallus is increased or decreased. Since even a cursory familiarity with receptaculitids indicates that there is a great deal of variation in the specific pattern of merome arrangement, a consistent procedure for pattern description will be a useful tool in comparative work.

The controversy surrounding the issues of life orientation and morphogenesis of receptaculitids has two principal roots: 1) divergent interpretations of particular aspects of morphology; and 2) attention to very different types of evidence, in the context of different taxa, by different workers. This second factor might have facilitated, rather than confused, efforts to develop a comprehensive understanding, except for the fact that there has not been an adequate basis for comparing the results of independent investigations. In other words, there has been abundant disagreement on what

features are in fact homologous on various receptaculitid thalli. This has made it difficult or impossible for workers to agree even on what would be a consistent orientation for all receptaculitids (e.g., Campbell et al., 1974, p. 68, discussing the work of Rietschel, 1969, and Nitecki, 1969), not to mention the problem of deciding whether or not such an orientation actually represented the life position.

It should go without saying that in order to develop a consistent and broadly applicable theory of homology, we need a detailed knowledge of the morphology of receptaculitid taxa representing as much as possible of the morphological spectrum which is actualized by the group. Yet this has not really been the thrust of most recent work. Rietschel (1969) makes an important contribution here, with his relatively complete characterization of the apical and basal regions of *R. neptuni*-like receptaculitids, but he considers a rather narrow range of body form. Studies of individual taxa are certainly important (Campbell et al., 1974; Gould and Katz, 1975), for it is on that level that the basic evidence on orientation and relative merome age must be gathered. However, these studies need to be synthesized through comparative work.

A key element in the development of the comparative morphology of receptaculitids will be the description of material that is sufficiently well preserved to provide information both on the surficial organization of merome plates and on features situated more proximally within the thallus. This will allow the determination of homology to be based on multiple lines of evidence, and will also make it possible to incorporate evidence from taxa for which our morphological understanding is clearly incomplete. We see the description of *I. dixonensis* as a contribution to this goal. The actual formulation of a theory of homology will be treated separately (Fisher and Nitecki, in prep.); our present aim is only to set forth the detailed morphology of this particular ischaditid and establish the basic context within which our research is undertaken.

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